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THE EVOLUTION OF THE SEX ORGANS OF PLANTS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LV.

FLORENCE LYON.

(WITH SIXTEEN FIGURES)

WITHIN the last twenty-five years there have been repeated attempts to bridge the chasm between the bryophytes and algae, but no transitional stages have been found between the unicellular sex organs of the green algae and the multicellular archegonium and antheridium of the bryophytes.

Morphologists have persistently fixed their attention upon the Chlorophyceae in their search for ancestral conditions, and have regarded the brown and red sea-forms as aberrant. Perhaps this is because no bryophytes, so far as is known, occur in salt or brackish water, and but few forms of brown algae exist in fresh. More likely, the attention focused on the alternation of generations, and the suggestion of an antithetic sporophyte and gametophyte in Coleochaete, Oedogonium, and Ulothrix, have been so dominant that the other groups have been set aside as unfruitful fields for investigation. All morphologists of note have laid stress upon the development of the sex cells and the sex organs as of the greatest importance in determining any theory of evolution. While the vegetative part of the gametophytes of bryophytes and pteridophytes is most changeable, appearing in many bizarre forms in the leafy jungermannias and the mosses, and varying from thin sheets of cells of the most primitive sort to tuberous bodies with highly differentiated tissues in the club mosses, simulating those of the higher plants, the sex organs of a group retain, as a rule, a constant monotonous type, varying from one another in related genera only in unimportant details, such as the length of the neck, the presence or absence of a stalk, the total emergence, or the whole or partial submergence of the archegonium in the vegetative tissues.

In the course of conducting university classes in general morphology for the past few years, I have had occasion to examine many preparations of representative plants of the chief groups, and have become impressed by the comparative frequency of certain irregularities in the development of the sex organs, particularly in pteridophytes, that show their plasticity and are suggestive from the evolutionary standpoint. I am inclined to look upon the "monstrosities," as biologists are fond of calling organisms which do not conform to a morphological rule of thumb, as presenting hints of ancestral conditions which afford at least a logical theory of the origin of the sex organs.

In a recent paper on the "Origin of the archegonium," Davis (1) has given a series of diagrams of hypothetical transitional forms to illustrate his view of the evolution of the sex organs from a plurilocular sporangium similar to that of *Ectocarpus virescens*. His theory would be far more convincing had he cited actual rather than hypothetical transitional forms, and such evidence is not difficult to obtain.

In an article on the development of the archegonium of mosses, Hy (2) describes an organ of mixed sexual character which has the egg apparatus at its base, and is distinctly spermatogenous at the summit. This phenomenon, he says, is not uncommon, occurring in several species — notably in *Atrichum undulatum*. Unfortunately he gives no figures of this interesting variation. Many instances of a similar nature in *Mnium cuspidatum* were observed by students in the Hull Botanical Laboratory two years ago, and figures of bisexual organs from this material appeared in Holferty's (3) paper in the February number of the BOTANICAL GAZETTE. None of the plants in that collection was mature enough to determine the future of the gametes, or whether the sperms were actually formed.[1] That the tissue appearing in a single organ consisted of immature cells of two kinds there can be no doubt. That antheridium and archegonium are homologous organs is a logical conclusion from the fact that cells at the apex of a moss shoot may indifferently develop into male, female, or bisexual organs. Further evidence to support this view of the homology of the sex organs, and that the simple axial row of an archegonium is reduced from forms which had two or more, is furnished by several groups of pteridophytes.

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[1] Since the above was written, specimens have been secured with perfectly typical moss sperms which were discharged from the antheridial region above the egg.

In three species of Equisetum (*E. hiemale*, *E. arvense*, *E. limosum*), the archegonium frequently consists of an egg, a shallow ventral canal and two neck canal cells pyriform in shape and lying side by side (*fig. 1*). Jeffrey (4) regards an archegonium of this form as typical. In his monograph he figures *E. arvense* and *E. hiemale* with two neck canal cells in this position, and the text calls attention to this characteristic.

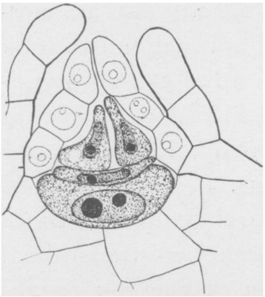

FIG. 1.—Longitudinal median section of archegonium of *Equisetum limosum*, showing the lateral position of the neck canal cells.

I have a few specimens showing the same conditions in *Isoetes lacustris* (*fig. 2*). Campbell (5) found two laterally placed nuclei in the single neck canal cell of *Isoetes echinospora* with no intervening wall.

Occasionally a division of the lowermost cell of the axial row, probably the "central" cell, occurs in *Selaginella apus*. This possibly may be interpreted as an egg and a ventral canal cell laterally placed (*fig. 3*). That they may both function as eggs seems evident from the case of polyembryony shown in *fig. 4*.

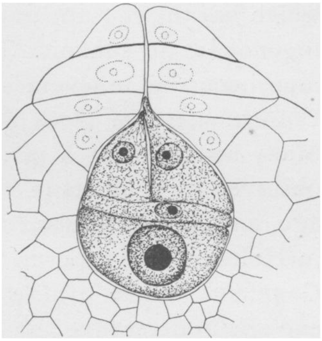

FIG. 2.—Longitudinal median section of an archegonium of *Isoetes lacustris*, showing lateral position of the neck canal cells.

But much more striking are the sex organs of at least two species of Lycopodium. It will be remembered that the gametophytes of only eleven species of this genus have ever been discovered, and that these differ so markedly among themselves as to be divided by Pritzel into five categories. They range from the simplest to the most complex gametophytes known, with the possible exception of certain mosses. I have a prothallus of *Lycopodium complanatum* bearing fifty or more archegonia; of these more than half have binucleate canal cells, and there are two instances in which the egg cell is included in the doubling (*fig. 5*). The remarkable number of cells in the axial row (often 14–16) marks these as unique amongst known archegonia of the imbedded type. I do not recall that Bruchmann (**6**), to whose notable work we are indebted for the knowledge of the gametophytes of this and other European species of Lycopodium, mentions the multiplication of the fertile cells, although one of his figures certainly shows it; but Treub (**7**) lays stress on the fact that the canal cells of *Lycopodium Phlegmaria* show a marked tendency to form two axial rows. I have taken the liberty of copying two of his figures (*figs. 6, 7*). Treub says that he frequently found archegonia of this sort, and all of his figures show it. He observed an interesting "monstrosity" twice. This was an archegonium whose upper neck canal cells increased to an abnormal number and were spermatogenous in character. He neglected to illustrate this duplex organ, but in this connection he recalls the similar phenomenon referred to by Hy (**2**) in mosses, and regards it as of importance. In all these variations there has been a tendency to increase the number of fertile cells by a lateral multiplication of the axial row.

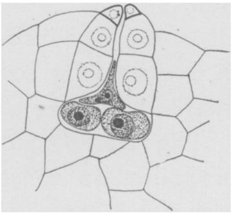

FIG. 3.—Longitudinal median section of an archegonium of *Selaginella apus*, showing lateral position of egg and ventral canal cells.

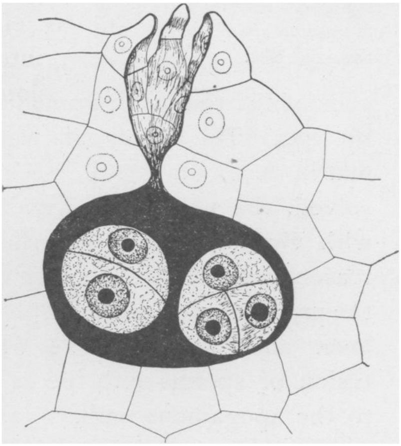

FIG. 4.— Longitudinal median section of archegonium of *Selaginella apus*, showing embryo derived from egg and ventral canal cells.

In quite another category is the archegonium of *Adiantum* *cuneatum* (*fig. 8*). Here two eggs are separated by two ventral canal cells lying below the two typical neck canal cells. Coker (8) has described and figured an archegonium of *Mnium* sp. with two eggs lying one above the other and each with a ventral canal cell. A *Funaria hygrometrica* preparation in my possession also shows this variation.

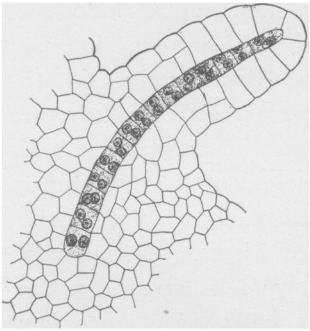
FIG. 5.—Longitudinal median section of an archegonium of *Lycopodium complanatum*, showing the lateral multiplication of the cells of the axial row.

The sex organs of some fern prothalli[1] gathered in an Indiana bog last summer display remarkable plasticity of form and character. The sex organs were developed in profusion on these prothalli, and the mat as it was stripped off a log appeared beset with young sporophytes. Everything in their appearance bespoke most luxuriant growth. Upon sectioning this material, the number of embryos formed from the sexual spores was found to be limited. Many of them are apogamous, developing most frequently from the "jacket" cells of the thallus in immediate contact with the egg. The archegonia were perfectly normal in development, the neck canal cells dissolved, the neck opened and became choked with vigorous-looking sperms, but for some reason in most cases the egg failed to become the progenitor of the sporophyte. I have not been able to determine whether there is fusion of sperms with the cells that give rise to the apogamous embryo, although there is some evidence of that condition. The archegonium neck behaves peculiarly. Instead of breaking down or becoming brown, as is the ordinary rule, in certain cases the lowermost neck cells branch and develop rhizoid-like filaments or even antheridia which mature

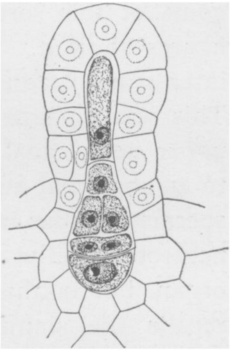
FIG. 6.—Longitudinal median section of an archegonium of *Lycopodium Phlegmaria*, showing the "doubling" of the axial row.—After TREUB.

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[1] The species was undetermined. In the immediate vicinity were growing three species of Osmunda. Probably the gametophytes belong to this genus.

and whose sperms have every appearance of being normal. The number of sperms produced, however, may be smaller than usual. Sometimes two or three antheridia are developed from the neck cells of the same archegonium (*fig. 9*). This is cogent evidence that the cervical cells of an archegonium are sterilized gametogenous cells which may regain potentiality. Goebel (9) describes the same phenomenon of antheridia developing from the neck cells of archegonia of *Hemionitis palmata* and *Lygodium japonica.* He comments thus: "Wir können dieses Verhalten als eine Alterserscheinung betrachten." But that can hardly be the explanation of the phenomenon in this case, for the prothalli were young and displayed unusual vigor. All stages of archegonia and antheridia appear in a single thallus.

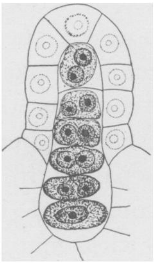

FIG. 7.—Longitudinal median section of an archegonium of *Lycopodium Phlegmaria,* showing two rows of neck canal cells.—After TREUB.

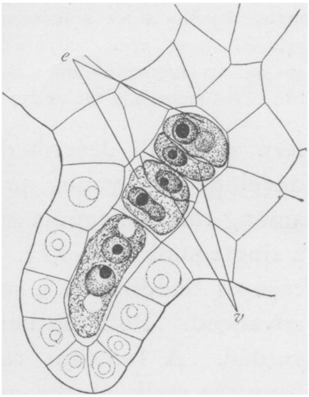

FIG. 8.—Longitudinal median section of an archegonium of *Adiantum cuneatum,* showing double egg apparatus: *e,* eggs; *v,* ventral canal cells.

Aberrant antheridia have been less frequently noticed. The form of the male organ seems to be singularly simple and monotonous throughout the bryophytes. I have found a variation of frequent occurrence, however, in the antheridium of *Atrichum angustatum.* The spermatogenous cells are separated into two groups by a transverse septum consisting of a single layer of cells formed from fertile cells that ceased to divide early in the development of the organs, and at about the period at which the wall is differentiated. Sometimes these two groups matured *pari passu;* again, the sperms were ready to escape from the upper or under chamber indifferently, while the other group was immature (*fig. 13*). This division of the sperm mass is the rule in *Selaginella apus* either with or without the intervening diaphragm as in Atrichum and in certain Hydropterideae. As is well known, at the moment of the development of an antheridium, when the wall is delimited from the potential spermatogenous cells, the latter are few in number and their walls become so much thicker than those which appear in their subsequent divisions, that the mature organ in section displays conspicuous plots, which frequently mature at different periods. Not rarely one or more of these cells fails to produce the same number of generations as the others, and so certain large spherical cells (for they separate from one another) may sometimes be found intermingled with mature sperms (*fig. 10*). I am inclined to regard these as eggs. Campbell reports budding of "secondary" antheridia from the stalk of an older Anthoceros antheridium, and the same thing has been seen in this laboratory. This variation is analogous to the formation of antheridia from the neck cells of the fern archegonia.

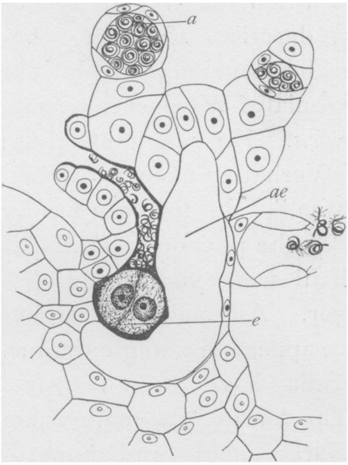

FIG. 9.—Longitudinal median section of "monstrous" fern archegonium, showing three antheridia developed from neck cells (*a*), an apogamous embryo(*ae*), and a normal two-celled embryo in the venter (*e*).

The antheridia of the apogamous fern prothalli described above were also *sui generis*. Those developed in young prothalli were typical. But those formed among the archegonia were frequently double, two antheridia on a single stalk (*fig. 11*). Upon investigation, this proved to be a case of budding of a secondary antheridium from another well advanced. Both antheridia produced perfect sperms that were voided. A frequent variant on this was a rhizoid-like branch from the stalk of the antheridium. A most interesting case of apogamy was observed twice. In these cases the embryo was formed from the stalk cell of an *antheridium!* This has not been observed, I think, by Lang (10) or any other investigator who has worked on apogamy.

In this connection and *à propos* of this unstable and plastic condition of the sex cells the preliminary announcement of apogamy in *Selaginella rupestris* may be made. It may be recalled that this is the form of Selaginella with a reduced number of functional megaspores (one or two) which are not shed until the embryo is fully equipped with leaves and root. In certain localities, the microspores are rarely produced and the embryos are frequently formed from the initial cell of the archegonium. Until the third or fourth division of this initial, it is impossible to determine whether a normal archegonium will result or an embryo.

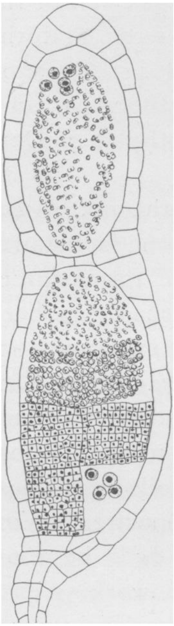

FIG. 10.— Antheridium of Atrichum, showing two chambers.

The development of the antheridium of the Anthoceros group has until recently been looked upon as unique. The male organ of no other group is known to arise from a hypodermal cell. The fact that this antheridium, sunken below compact tissue, has a well-developed wall, militates against the view that it is a primitive form. Emma Lampa (**11**) has noted Anthoceros plants which develop emergent antheridia arising from superficial cells, similar to those of other groups of liverworts, and believes them to be a reversion to an ancestral form. I do not regard them in the same class with the sunken sex organs of Lycopodium, Botrychium, Phylloglossum, Equisetum, and the archegonia of Selaginella, Isoetes, and Anthoceros, which have no sterile jacket. These, to my mind, represent a different line of evolution from the emergent sex organs with long necks and stalks. Davis's theory of the pluriculocular sporangium-like body of a definite form and bisexual character, essentially an emergence of fertile tissue from the surface of a hypothetical thallus body which came to

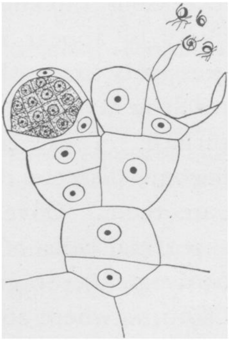

FIG. 11.— Branching antheridia of Osmunda (?).

adopt the land habit, seems to account plausibly enough for the *emergent* archegonium and antheridium of the Marchantia and moss type, but it is less convincing as the ancestral form of sunken sex organs, particularly those which have "lost" (?) stalk, wall, and other sterile cells except the cover. The sunken sex organs of all plants develop from an epidermal cell of the *dorsal* surface of the gametophyte, except in ferns and the Anthoceros forms, in which they are frequently produced on both dorsal and ventral sides. This is true of Anthoceros, but I know of no authority that it is the case in Notothylas or Dendroceros.

In speculating upon the early development of the sex organs and the significance of the variations noted above, one fact stands out prominently, that the cells concerned in the formation of the sex organs are more plastic and indifferent than has been believed, and that the region giving rise to the sex organs not infrequently displays a latent gametogenous character. One might go back further to a stage preceding the emergent plurilocular sporangium and postulate as a point of departure thallose algae with indeterminate masses of reproductive cells which pass through the plant from one surface to the opposite. With increasing thickness of the thallus, sterilization will be most likely to appear at the center of the mass and, working progressively from the center outward in both directions, would result in layers of gametogenous or sporogenous cells at each surface. These concrete masses by further sterilization might become discrete patches or "organs," if one chose so to designate them. Cover cells would arise from sterilization of the superficial cells of these regions. Up to this point there might be isogamy, or even the indefinite condition that obtains in Ulothrix, where zoospores cannot be distinguished from gametes. Differentiation of sex cells could be accounted for by certain cells ceasing to divide earlier in their development than others, resulting in eggs, as contrasted with those that by repeated divisions work out sperms. In this way some of the primitive organs in all probability would be bisexual. The emergent sex organs could evolve from these sunken forms by pushing the sterilization idea further and considering eruptions to arise from the thallus. This fertile branch could easily evolve into an archegonium or an antheridium, or an organ of mixed character.

But however fascinating and probable a scheme of evolution is, it deserves scant attention unless it can muster at least circumstantial evidence to support it. Illustrations of all the phases which I have suggested may be readily found among the algae, especially the browns. *Ulva lactuca* is a thallose green alga which consists of two layers of cells throughout, except at the period of reproduction, when irregular masses of these cells subdivide into gametes with two cilia, or zoospores with four. Thus in certain regions the thallus becomes eight or even sixteen layers of cells thick, all of these being fertile (*fig. 12*). *Phyllitis caespitosa* consists of sterile cells in the central region of its thallose body, while the layer of cells on each surface subdivides into gametogenous or sporogenous cells (*fig. 13*). *Punctaria latifolia* has patches of these cells separated into primitive organs by sterile tissue (*fig. 14*). Moreover, these patches are distinctly of two sorts, the one consisting of few large cells, the other of small cells which discharge sperms said to fuse with the larger cells (eggs ?). Zanardinia has exogenous sex organs of two kinds (*fig. 15*). The branching of the male sex organs is of interest and may suggest a clue to that aberration in Anthoceros, Mnium, and the ferns hitherto

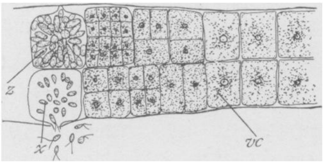

FIG. 12.—*Ulva lactuca:* dorsiventral section of thallus, showing vegetative cell (*vc*), cells in process of forming zoospores and mature zoospores of two sizes (*x*, *z*). Diagrammatic.

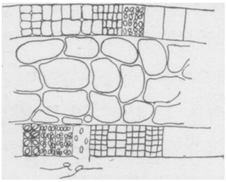

FIG. 13.—*Phyllitis caespitosa:* dorsiventral section of thallus, showing reproductive cells at both surfaces; sporangia form a continuous layer on each.—After RIOCREUX.

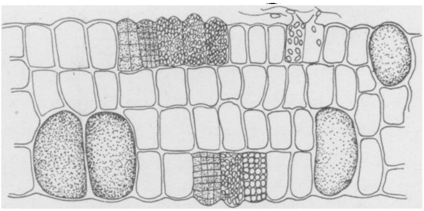

FIG. 14.—*Punctaria latifolia:* dorsiventral section, showing sexual cells in patches on both surfaces.

described. In his anatomical study of Porphyra, Janczewski (**12**) describes the two sorts of sexual cells produced, the "antherozoids" and the "octospores," and says that he considers the latter as antheridia whose final segmentation has been arrested. He says further: "Je considère comme une *anthéridie* le groupe d'*anthérozoïdes* siégeant dans une maille du réseau, correspondant à une octospore, et issu par conséquent d'une cellule végétative. Le développement des anthéridies est d'abord tout à fait semblable à celui des octospores. Il obéit ensuite aux mêmes règles, et l'on dirait que les octospores ne sont que des anthéridies dont la segmentation ultérieure a été arrêtée."

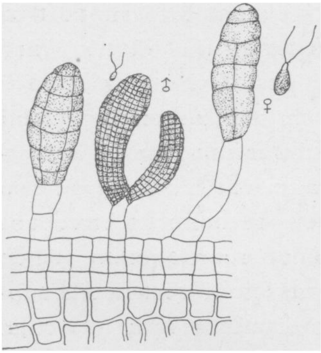

FIG. 15.—Portion of dorsal surface of Zanardinia, showing the emergent sex organs.

This view suggested to me that the conditions sometimes found in a bryophyte antheridium might be analogous or even homologous. Are the cells which are arrested in division and assume a spherical shape (*fig. 10*) homologous with eggs, and is their appearance a return to ancestral condition?

The theory I have outlined would account for sex organs on or near both dorsal and ventral surfaces, as they are known to occur in Anthoceros, in certain thallose jungermannias, and in ferns. It would explain the sunken sex organs consisting of fertile cells not surrounded by a wall, formed of sterile sister cells, as the archegonium of Anthoceros and the antheridia of Equisetum and Lycopodium. According to such a theory, existent transitional stages might be expected in which the sex organs would not have assumed a definite shape nor a definite number of cells. Precisely this indeterminate condition is to be found in certain

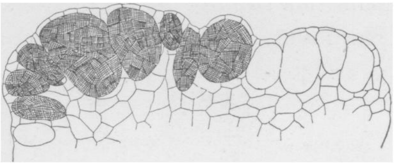
FIG. 16.—*Lycopodium annotinum:* dorsiventral section of portion of gametophyte, showing antheridia of indeterminate size and shape.

species of Lycopodium, notably *Lycopodium annotinum* (*fig. 16*), in which the antheridial region is made up of patches of spermatogenous cells quite indefinite in contour and varying in number. There is no wall of sterile cells. This appearance is not due to difference in state of development, or because antheridia are cut in different planes, as might be inferred from a single section. I have seen antheridia at maturity varying in the number of sperm cells from fifty to more than three hundred. Not infrequently groups of spermatogenous cells derived from separate initial cells abut upon one another with no intervening cell tissue, but it is generally easy to trace the individual groups. Sex organs of this type are logicallv explicable by the progressive sterilization of an indefinite superficial region, but it requires a *tour de force* to imagine the modification of an emergent sporangium of definite form into the sunken condition displayed by Lycopodium.

Archegonia and antheridia of few cells are generally regarded as the most advanced. From this standpoint, the sex organs of this species of Lycopodium are the most primitive ones known. This of course does not take into consideration the anomalous bisexual organs of *Mnium cuspidatum* described by Holferty. On the other hand, no gametophyte, with the exception of certain mosses, is so complex in the variety and specialization of its vegetative tissues as that of *Lycopodium complanatum* or of *Lycopodium annotinum.* To be sure, the gametophyte of *Lycopodium cernuum* by contrast is exceedingly simple, and that of Phylloglossum is said by Thomas (13) to show little internal differentiation of cells; but cases are frequent among animals where somatic tissues become elaborate and highly organized, while the sex organs lag behind and retain great simplicity. This would be expected in organisms where the struggle for existence is great, as it may have been among the Lycopodiums, if one may judge from the capricious germination of the spores. Moreover, the symbiotic relation of the club mosses with a fungus indicates difficulties in development. Attempts have been made repeatedly to germinate the spores of the club mosses, but the results obtained thus far have been unsatisfactory. The life history of every gametophyte of Lycopodium now discovered is full of gaps.

Several years ago, in his brilliant monograph on the evolution of the sporangium, Bower (14) suggested that emergences erupted from an indefinite concrete imbedded mass of sporogenous cells, and by progressive sterilization and branching resulted in discrete sporangia. In support of his view, he marshaled existent bryophyte and pteridophyte forms that he regards as analogous to those that may have appeared in the direct line of evolution. The same kind of argument may be applied to the origin of the sex organs. I have no idea that any of the brown or red algae represent lineal ancestors of the liverworts or ferns as we now know them; but if the Phaeophyceae are perchance an offshoot from green algae, the method in which they produce their reproductive cells may be like that of their forbears, from whom also the archegoniates have probably evolved. It is possible that the investigations of apogamy now proceeding will throw some new light on the subject. I hazard the suggestion that the origin of the apogamous sporophyte is among latent gametogenous cells of the thallus, which under unknown conditions develop sporangia without the formation of sex organs. Such a hypothesis may seem rash, but there is, I think, no inherent improbability in the theory, while it furnishes a suggestive line for investigation among the brown algae, which is a sufficient reason for its being. If Farmer's (15) preliminary announcement of the fusion of the nuclei of neighboring cells of fern prothalli, as a step preliminary to the formation of the apogamous sporophyte, is confirmed, are these fusing cells to be regarded as stable vegetative cells, or as potential isogamous gametes? If the latter, is it not conceivable that they are surviving cells of a former fertile region which normally are sterile, but on occasion may regain potentiality?

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LITERATURE CITED.

1. DAVIS, B. M., Origin of the archegonium. Annals of Botany 17: 477–492. 1903.
2. HY, F., Recherches sur l'archégone et le développement du fruit des Muscinées. Ann. Sci. Nat. Bot. VI. 18: 121. 1884.

3. HOLFERTY, G. M., The development of the archegonium of *Mnium cuspidatum.* BOT. GAZ. **37**: 106–126. *pls. 5–6.* 1904.
4. JEFFREY, E. C., The development, structure, and affinities of the genus Equisetum. Mem. Boston Soc. Nat. Hist. **5**: 155–190. 1899.
5. CAMPBELL, D. H., Contributions to the life history of Isoetes. Annals of Botany **5**: 231–258. 1891.
6. BRUCHMANN, H., Über die Prothallien und Keimpflanzen mehrerer europäischer Lycopodien. Gotha. 1898.
7. TREUB, M., Recherches sur les Lycopodiacées. Ann. Jard. Bot. Buitenzorg **4**: **5**: **7**: **8**: 1884–1890.
8. COKER, W. C., On the occurrence of two egg cells in the archegonium of Mnium. BOT. GAZ. **35**: 136. 1903.
9. GOEBEL, K., Organographie der Pflanzen 400. 1901.
10. LANG, W. H., On apogamy and the development of sporangia upon fern prothalli. Phil. Trans. Roy. Soc. London B. **190**: 187–238. 1898.
11. LAMPA, EMMA, Exogene Entstehung der Antheridien von Anthoceros. Oesterr. Bot. Zeits. **53**: 436–438. 1903.
12. JANCZEWSKI, E., Études anatomiques sur les Porphyra. Ann. Sci. Nat. Bot. V. **17**: 241–260. 1873.
13. THOMAS, A. P. W., Preliminary account of the prothallium of Phylloglossum. Proc. Roy. Soc. London **69**: 285–291. 1901.
14. BOWER, F. O., Studies in the morphology of the spore-producing members. Phil. Trans. Roy. Soc. London B. **185**: 473–572. 1894.
15. FARMER, J. B., MOORE, J. E. S., and DIGBY, L., On the cytology of apogamy and apospory. I. Preliminary note on apogamy. Proc. Roy. Soc. London **71**: 453–457. *figs. 4.* 1903.